

BATRACHOSPERMACEAE (RHODOPHYTA) IN FRANCE:
200 YEARS OF STUDY

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ABSTRACT — Documentation of the Batrachospermaceae, a family of freshwater red algae, began in France in 1797. Much of the nomenclature in this family is based on the excellent herbarium specimens of J.-B.G.M. Bory de St-Vincent (1778-1846) and S. Sirodot (1825-1903). The recent morphometric-based system of R.G. Sheath, M.L. Vis and K.M. Cole has rationalized the multitude of names associated with these specimens. The Batrachospermaceae holdings of PC are here tabulated and cross-referenced to this system, and collections made by the author in 1992 are used to test the species concepts. Further collecting in France is recommended to assess environmental change and rarity, and to improve our concepts of taxa and taxonomic characters in the Batrachospermaceae.

RÉSUMÉ — La documentation sur les Batrachospermacées, une famille d'algues rouges d'eau douce, a commencé en France en 1797. La nomenclature de cette famille est, en grande partie, basée sur les excellents échantillons d'herbier de J.-B.G.M. Bory de St-Vincent (1778-1846) and S. Sirodot (1825-1903). Le nouveau système de R.B. Sheath, M.L. Vis et K.M. Cole, basé sur la morphométrie, a rationalisé la multitude des noms qui leur ont déjà été attribués. Un état des échantillons de *Batrachospermum* conservés à PC est dressé, sous la forme d'un tableau dans lequel ceux-ci sont rapportés à ce système. Les échantillons récoltés en France en 1992 par l'auteur lui-même sont analysés pour vérifier les concepts d'espèces. De nouvelles récoltes en France sont souhaitables pour estimer les modifications de l'environnement, pour évaluer la rareté de certains taxons et pour améliorer nos concepts taxonomiques ainsi que les caractères sur lesquels ils reposent chez les Batrachospermacées.

KEY WORDS: *Batrachospermum*, freshwater red algae, history, nomenclature, taxonomy, systematics

INTRODUCTION

The purpose of this paper is three-fold: firstly, to provide a brief overview of the documentation of France's Batrachospermacean flora; secondly, to test the taxonomic system of Sheath and colleagues using contemporary collections from France; and thirdly, to draw some general conclusions about the abundance of species in France. In so doing,

I wish to honour Professor Pierre Bourrelly, whose books inspired me as a student to study freshwater algae, and since then have been invaluable companions in my studies.

HISTORICAL BACKGROUND

1797-1823: At the age of eighteen and in the fourth year of the First Republic, Jean Baptiste Geneviève Marcellin Bory de Saint-Vincent (1778-1846) submitted a paper to the Société d'Histoire Naturelle de Bordeaux on the Linnaean genera *Conferva*, *Byssus* and *Phytoconis*. In that paper (1797), Bory described the species of these genera reported from the department of Gironde (Bory was Conservateur des Collections in the Société). Based on his own observations, he provided the first detailed description of *Conferva gelatinosa*. This species, he noted (on p. 38), was perhaps distinct enough to be separated from *Conferva*. In fact in Germany, in the same year, Albrecht W. Roth (1797) established the genus *Batrachospermum* to include *Chara gelatinosa* (L.) Roth [syn. *Conferva gelatinosa* L. (in error by Roth as "*Conferva nodosa* L.")] and *Chara batrachosperma* Weiss. Bory also recognized several variétés of this taxon, two of them growing in Gironde and matching Dillenius's (1741) *Conferva...major et fusca* and *Conferva...minor et viridis* (both = *Batrachospermum gelatinosum sensu Vis et al.*, 1995).

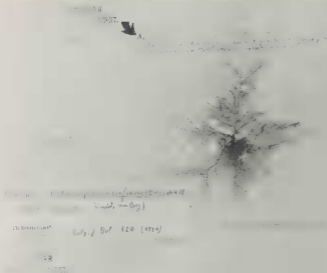
Bory was fascinated by freshwater red algae. While serving in Napoleon's army, he collected throughout Europe, including in 1802 the department of Ille-et-Vilaine (destined to become the geographical heart of *Batrachospermum* taxonomy upon publication of Simon Sirodot's monograph in 1884).

In 1808, Bory published three papers on the Batrachospermales. The first paper (1808a) concerned the genus *Thorea*. In his second (Bory 1808b), Bory includes among the six species of *Lemanea*, *L. sertularina*, *L. dillenii* and *L. batrachosperma*, all "setaceous" species of *Batrachospermum*. Collections were provided by compatriots such as D.S. Léman, J. Thore and J.P.R. Draparnaud. In his papers, as in his herbarium, new species are designated with a capital "N".

Bory's (1808c) third paper concerned the genus *Batrachosperma*. He includes the species *B. bambusina*, *B. helmintosa*, *B. ludibonda* (incl. "varieties" *confusa*, *aequinoxialis* from Réunion, *moniliforma*, *pulcherrima*, *ca[æ]erulescens*, *viridis*, *stagnalis*), *B. turfosa*, *B. keratophyta* and *B. tristis* (= *Draparnaldia*; incl. "varieties" *chlora* and *colorata*).

In 1823, Bory transferred the three species of *Lemanea* mentioned above to *Batrachosperma* (the latter becoming *B. tenuissima*). An additional species, *B. hybrida*, is described, and *caerulescens* is raised to species level. Bory's fine herbarium (e.g. Fig. 1) was purchased by Gustav A. Thuret and now forms part of the collection at PC.

1867-1884: Simon Sirodot (1825-1903), school teacher, botanist and finally academic, discovered phycology relatively late in life. While Professor of Botany and Zoology at the Université de Rennes in the 1860s, his research assistant and bryologist, Jules Gallée, encouraged his interest in *Batrachospermum*. Sirodot's own collections were limited by how far he could travel by stagecoach (F. Magne, pers. comm.), but by 1873, when he described the sections *Moniliformia*, *Turfosa*, *Helminthosa* and *Virescentia*, he was intimately acquainted with the *Batrachospermum* flora of France. His own collections from north-western France were supplemented by the rich herbarium legacy of Bory and his compatriots. Sirodot's splendid monograph of 1884 is a fitting memorial to what became his life's work.



a. Batrachosperma ludibunda (confusa) griseo-fusca, verticillis contiguis, subconfusis, supernis et inferis compressis. N.

N.º 637 Gir. chartrans. Mycos. p. 175. pl. XXV. (Mousses).



Cette variété n'est point rare; elle croît dans le bassin fermé des fontaines très-pures et froides. Elle y semble choisir les lieux obscurs. On la trouve dans les trous des feux dont les eaux ne charient aucun limon. Je l'ai observée en France, en Espagne, en Allemagne, en Pologne et dans la Prusse Ducale.

De toutes les batrachospermes, celle-ci acquiert les plus fortes dimensions; sa longueur est quelquefois de quatre pouces et demi, son diamètre égale souvent celui du chancre des granulés. Ses rameaux paroissent aussi moins étalés que dans les variétés suivantes. Les globules ou verticilles sont si rapprochés et si gros, qu'ils se confondent souvent, de sorte qu'on les distingue à peine dans certains individus qui ont en peu l'aspect du *Batrachosperma helomentosa*. La couleur de la plante est d'un gris-bleu-noir agréable par sa transparence; les grâces signifient un peu sur le jaunâtre. Ces tentes deviennent d'un assez beau violet par la putréfaction.

Bot. t. 10110 1

Batrachosperma ludibunda (Bory) Hassall
N.º 637 Gir. chartrans. Mycos. p. 175. pl. XXV.

Fig. 1. *Batrachosperma ludibunda [ludibunda] confusa* Bory: Environs de Fougères en Bretagne, France, an VIII [1799-1800] (PC, Herbarium Thuret). Holotype of *B. confusum* (Bory) Hassall.

Paris 27 mai 1882



Fontaine de Châtillon, commune de Bruz,
près de Rennes. 27 mai 1882.

SIRODOT BEDT.

B. Bruziense Sirodot!

F. 1882

Fig. 2. *Batrachospermum bruziense* Sirodot: Fontaine de Châtillon, commune de Bruz, près de Rennes, 27 Mai 1882 (PC, Herbarium Thuret). Middle specimen designated lectotype in Sheath *et al.* (1994a).

Sirodot made a number of nomenclatural errors (e.g. creating later synonyms and homonyms, and altering the ending of sectional names) but his monograph remains the only Flora of *Batrachospermum* for France. Hamel (1925) provides essentially a condensed version of Sirodot (1884) with some additional collections. Most of Sirodot's herbarium is housed at PC, and all specimens are adequately labelled and preserved (e.g. Fig. 2).

The twentieth century: Sirodot's species concepts were refined by Kylin (1912) and then more substantially challenged by Israelson (1942). Skuja added considerably to our knowledge of the family Batrachospermaceae (e.g. Skuja, 1931, 1944) but failed to complete his proposed world monograph. In the last few decades, beginning with Mori (1975), there has been a major reassessment of species concepts and a reexamination of types (e.g. Compère, 1991; Kumano, 1990; Necchi, 1990; Vis *et al.*, 1995). The recent revisionary work of R.G. Sheath, M.L. Vis and K.M. Cole (Sheath *et al.*, 1993, 1994a, 1994b, 1994c; Sheath & Vis, 1995; Vis *et al.*, 1995) used morphometric characters to rationalize (and greatly simplify) the taxonomy within the family, and particularly within *Batrachospermum* (Table 1).

Table 1. Nomenclatural and taxonomic changes in *Batrachospermum*

CURRENT NAME ¹	NAMES USED BY BORY & SIRODOT, 1808-1884	SPECIMENS FROM FRANCE HELD IN PC ²
Section <i>Batrachospermum</i>³	Sections <i>Moniliformes</i> & <i>Helminthoides</i>	
<i>anatinum</i> Sirodot	<i>anatinum</i> Sirodot <i>ectocarpum</i> Sirodot	31
<i>arcuatum</i> Kylin	—	17
<i>boryanum</i> Sirodot	<i>boryanum</i> Sirodot	11
<i>confusum</i> (Bory) Hassall	<i>crovanianum</i> Sirodot <i>helminthosum</i> Sirodot non Bory <i>ludibonda confusa</i> Bory	37
<i>gelatinosum</i> (L.) DC.	<i>corbula</i> Sirodot <i>decaisneanum</i> Sirodot <i>densum</i> Sirodot <i>godronianum</i> Sirodot <i>hybrida</i> Bory <i>ludibonda coerulescens</i> Bory <i>ludibonda pulcherrima</i> Bory <i>ludibonda stagnalis</i> Bory <i>moniliforme chlorosum</i> Sirodot <i>moniliforme helminthoidesum</i> Sirodot <i>moniliforme rubescens</i> Sirodot <i>moniliforme scopula</i> Sirodot <i>moniliforme typicum</i> Sirodot <i>pygmaeum</i> Sirodot <i>pyramidale</i> Sirodot <i>radians</i> Sirodot <i>reginense</i> Sirodot	290
<i>skujae</i> Geitler	<i>sporulans</i> Sirodot	7
Section <i>Hybrida</i>	Section <i>Hybrida</i>	
<i>virgato-decaisneanum</i> Sirodot	<i>virgato-decaisneanum</i> Sirodot	3

Section <i>Turfosa</i>	Section <i>Turricoles</i>	
<i>turfosum</i> Bory	<i>keratophytum</i> Bory <i>turfosum</i> Bory	59
	<i>vagum</i> (Roth) C. Agardh	
	<i>vagum keratophytum</i> (Bory) Sirodot	
	<i>vagum suevorum</i> (Kütz. <i>nom. illeg.</i>) Sirodot	
<i>vogesiacum</i> T.G. Schultz ex Skuja	<i>vagum flagelliforme</i> Sirodot	6
Section <i>Virescentia</i> (& <i>Setacea</i>)	Sections <i>Vertis</i> ■ <i>Setaces</i>	
<i>atrum</i> (Huds.) Harv.	<i>gallaei</i> Sirodot	93
	<i>dillenii</i> (Bory) Bory	
	<i>tenuissimum</i> Bory	
	<i>sertularinum</i> (Bory) Bory	
<i>elegans</i> Sirodot	<i>coerulescens</i> Sirodot	21
	<i>elegans</i> Sirodot	
<i>helminthosum</i> Bory non Sirodot	<i>bruziense</i> Sirodot	23
	<i>graibussoniense</i> Sirodot	
	<i>helminthosum</i> Bory non Sirodot	
	<i>testale</i> Sirodot	
	<i>virgatum</i> Sirodot	
	<i>viride</i> Sirodot	
Names of doubtful application		
? <i>vagum</i> [Skuja in sched.]	<i>vagum</i> var. <i>affine</i> (Kütz.) Sirodot	2
? <i>vagum</i>	<i>vagum</i> var. <i>refractum</i> Sirodot	?0
? <i>vagum</i>	<i>vagum</i> var. <i>vulgare</i> Sirodot	?0
<i>ascios</i> [axios] Skuja in sched.	—	1
<i>ectocarpoideum</i> Skuja in sched.	—	2
<i>myurus</i> DC.	—	2
<i>pulvinatum</i> Bonhomme	—	1

¹ The "current name" is taken from the series of papers by Sheath and co-workers (Müller *et al.*, 1997; Sheath *et al.*, 1993, 1994a, 1994b, 1994c; Sheath & Vis, 1995; Vis *et al.*, 1995).

² The figures are approximate and some mistakes will have been made through misreading labels and ignoring duplication among "subherbaria". However the numbers reflect the relative frequency of collections in PC and (hopefully) to some extent the frequency of taxa in the field. Collections are housed in "PC Herbar de France", "PC Herbar Thuret", "PC Herbar Montagne" or "Reliquae Sirodotianae". The determinations are those used in the herbarium (many by Heinrichs Skuja) and none have been confirmed.

³ The sections *Aristata*, *Contorta*, *Nothocladus*, *Sirodotia* and *Tuomeya* are not represented in France.

In France, the only major collections made this century were those included in the herbarium of E. Chemin (donated to PC), mostly by E. Cheuy in the 1930s. Sixty seven specimens of *Batrachospermum* are housed in the herbarium of the Université de Rennes, including material labelled "Reliquae Sirodotianae" in the "Fonds Gallée". The collection was curated by Francis Magne between 1965 and 1971, when he taught at the university and studied the life history and development of Lemnaceae from local

populations. All specimens collected by Sirodot and identified to species were transferred to PC.

Prior to Magne arriving in Rennes, Heinrichs Skuja had attempted to recollect from some of Sirodot's localities. Unfortunately the landscape had become much degraded, and Skuja was unable to find any *Batrachospermum* in the region (F. Magne, pers. comm.).

RECENT OBSERVATIONS

As part of a trip to France in 1992 to examine collections of Batrachospermaceae in PC, I too revisited some of Sirodot's collection sites near Rennes. Fortunately, I was able to find a few extant populations of *Batrachospermum*. I present these collections, and one from the Dordogne River valley in southern France, both as a test of the Sheath-Vis-Cole system (see above), as well as to stimulate further collecting in France to assess current day distributions.

Batrachospermum helminthosum Bory, *Ann. Mus. Hist. Nat.* 12: 316 (1808), non Sirodot (1884).

Specimen examined: Stream flowing into St-Malo-de-Beignon, Beignon-Launay Road, Paimpont region, 40 km SW of Rennes, route D124, 56-Morbihan, 2.x.1992, *Entwisle 2165* (MEL, PC).

Only young thalli were found, among "Chantransia" tufts in a heavily shaded creek. The carposporophytes are large and centrally inserted; the carpogonia symmetrically attached to the subtending cell and ca 45 µm long; the carpogonial branches straight, modified and ca 2 cells long; and the trichogynes pedicellate, cylindrical, and without knobs or branches. This combination of features matches *B. helminthosum sensu* Sheath *et al.* (1994a).

Distribution: Sirodot collected *B. helminthosum*, and current synonyms (Table 1), from many streams within a 50 km radius of Rennes. Although now reported from most continents (but not Australia) it has not been widely reported in France outside Brittany. The most recent collection in PC was also from Paimpont, in 1969.

Batrachospermum virgato-decaisneanum Sirodot, *Batrachospermes* 290 (1884).

Specimen examined: Le Meu River, Moulin de Dompierre, Trémoré, ca 50 km W of Rennes, route N164, 22-Côtes du Nord, 2.x.1992, *Entwisle 2167* (MEL).

A small, bright green fragment only was found at this site. With carpogonia ca 22 µm long and asymmetrically attached; trichogynes pedicellate and sessile; and the carpogonial branch 3-celled and modified, this collection is clearly referable to *B. virgato-decaisneanum*.

Distribution: This is the first record of *B. virgato-decaisneanum* from France since the collections of Sirodot in 1883. Sirodot reported it only twice, from near Montfort, 20 km W of Rennes. My collection was a fragment only and further searching for this species is warranted. *Batrachospermum virgato-decaisneanum* has been reported from elsewhere in Europe and also North and South America, Japan, Australia and New Zealand (Sheath & Vis, 1995; Entwisle, 1993). Although widespread, it is apparently uncommon worldwide.

***Batrachospermum confusum* (Bory) Hassall, *Hist. Br. Freshw. Algae* 1: 105 (1845).**

Specimens examined: Stream from Roc Trévezel into Réservoir de St Michel, Botmeur-la Feuillée Road, first river crossing E of Botmeur township, ca 10 km WNW of Huelgoat, route D42, 29-Finistère, 30.ix.1992, *Entwisle 2157* (MEL, PC); Le Meu River, below Forêt de la Hardouiniais, near Trémoré, ca 8 km W of St-Méen-le-Grand, route N-164, 22-Côtes du Nord, 2.x.1992, *Entwisle 2168* (MEL, PC).

The grey-olive thalli were attached to rocks in flowing water. Carposporophytes are numerous, small, and ca 14 cells from axis; spermatangia are borne on involucrel bracts; and rhizoidal filament cells are swollen in mature axes. These characters define *B. confusum sensu Vis et al.* (1995).

Distribution: Species now included under *B. confusum* were reported commonly by Sirodot from the region around Rennes, extending NW to Saint-Pol-de-Léon. The most recent collections in PC were made prior to World War II.

***Batrachospermum gelatinosum* (L.) DC., *Bull. Sci. Soc. Philomat. Paris* 3 (51): 21 (1801).**

Specimen examined (1): Small stream flowing out below Meyrals Chateau, St Cyprien-Meyrals-Sarlat Road, ca 2 km from St Cyprien, route D25, 24-Dordogne, 21.x.1992, *Entwisle 2176* (MEL, PC).

The thalli, growing with *Vaucheria* in a small pool, were grey, rubbery and *Chaetophora*-like in texture. With carposporophytes small and scattered through the whorls; carpogonia subtended by unmodified branches; rhizoidal filaments loose and tangled but the cells remaining cylindrical; and the population apparently monoecious (all individuals examined bore carpogonia, and spermatangia were observed attached to trichogynes), the collection is referable to *B. gelatinosum sensu Vis et al.* (1995).

Specimen examined (2): Le Buisson, ca 2 km SW of St-Malon-sur-Mel, Paimpont Forêt, 35-Ille-et-Vilaine, 2.x.1992, *Entwisle 2164* (MEL, PC).

This collection of small thalli from a slow-flowing stream was difficult to identify due to the rarity of key diagnostic features in a limited amount of fertile, new growth. Diagnostic features were as above, but the rhizoidal filaments were sometimes undulate or with an irregular surface (but the cells never inflated). Once again the only spermatangia observed were attached to trichogynes but all specimens observed bore carpogonia, so the population is assumed to be monoecious.

In older parts of the thalli, secondary fascicles were profuse and as long as primary fascicles, resulting in elongate, cylindrical whorls. This gross morphology is apparently unusual for European *B. gelatinosum* (see e.g. illustrations in Vis *et al.*, 1995), but not unexpected for "overmature" individuals of any species of *Batrachospermum*.

No unfertilized trichogynes were observed and most fertile branches were bearing carposporangia, even those with limited apparent gonimoblast development. These carposporangia were 6-8 µm long and globose to obovoid, not all that different in size and shape to the spermatangia attached to trichogynes. However, they seemed to be consistently bigger than the spermatangia and were always associated with fertilized trichogynes (but note that no unfertilized trichogynes were observed). Furthermore, if they were spermatangia, the collection would be allied with *B. pulchrum* which unlike *Entwisle 2164* has well-curled fascicles (Vis *et al.*, 1995). The most pragmatic approach is to refer this collection to *B. gelatinosum*.

Distribution: Although widespread throughout the world, *B. gelatinosum* has over the last century become less common on the Eurasian continent, particularly near large cities (Geissler, 1991; Usachjova, 1995).

DISCUSSION

At 13 species (using current concepts), the French Batrachospermaceae flora is not particularly rich. Recent field and herbarium studies in Australia, suggest that there are *ca* 25 species in that country. While Australia covers a broader range of climate zones than France, the greatest species diversity is found in the southern temperate zones. Of more interest than simple species tallies is the fact that there are few species shared by both countries: that is, there are many endemics in Australia. However, *B. gelatinosum* and *B. atrum* seem to be the most widespread and common of species in both countries (although current concepts may neglect important variability). Most species reported from France are also found in other northern hemisphere regions such as North America, a region which boasts a total of some 30 species. Nevertheless, the flora of France is of immense historical and nomenclatural interest. Phylogenetic relationships are not yet resolved in Batrachospermaceae so further biogeographic analysis is premature.

Post World War II collections of Batrachospermaceae from France are rare in PC, and apart from a brief flourish in the 1930s, there are very few collections from this century. However, the French Batrachospermaceae flora must be one of the best documented of any "plant" group for the nineteenth century. In particular, the flora of the Rennes region is extremely well vouchered. As one would expect, recent intensive sampling near large cities in Europe *sensu lato* (e.g. Berlin, Geissler, 1991; Moscow, Usachjova, 1995) has shown Batrachospermaceae to be extinct or threatened with extinction. Even more widely in Europe, the family appears to be rare or at least rarely sighted (e.g. Freidrich *et al.* 1984). As Freidrich *et al.* (1984) note, systematic collecting is needed to assess the current distribution and abundance of Batrachospermaceae in Europe. Systematic collecting throughout France, particularly concentrating of sites visited by Sirodot, would form the basis of a very useful comparative study. Changes in habitats over the last century or so should be reflected in the presence or absence of Batrachospermaceae species.

The system of Sheath and co-workers accommodated all collections documented here: deviations can be explained by the poor quality of the specimen. It is possible that new taxa will be discovered in France, particularly outside Brittany. It is also possible that further analysis of individual characters may show that the taxa defined by dissimilarity of multiple morphometric characters obscure phylogenetically and/or phenetically distinct entities. The character of monoecy vs dioecy, e.g., requires further study. Vis *et al.* (1995) include two "species pairs" that differ only (or almost only) in this regard. This character, with the two states monoecious and dioecious, has no *intrinsic* value taxonomically or phylogenetically (despite the impassioned pleas of e.g. Proctor, 1975). In a study in progress, we find this simplistic scoring of the character inadequate, and its suitability as a taxonomic character suspect in many instances. Devaluing this character would result initially in fewer species being recognized, but an assessment of all vegetative and reproductive features may result in the discovery of more informative characters. Also, the distribution of female and male gametangia may in fact provide a number of more complex characters that can be better used to interpret phylogeny. To improve our knowledge of diversity and relationships, we need to analyse the development, distribution and evolution of characters.

ACKNOWLEDGEMENTS — André Kermarrec (Université de Rennes) very kindly sent complete details of the *Batrachospermum* holdings of the Université de Rennes herbarium. Drs Alain Couté and Bruno de Reviers and Professor Pierre Bourrelly assisted me in my study of PC herbarium material, and Dr Francis Magne provided information and helpful comments on the manuscript. The Maud Gibson Trust, Sydney-Illawara Water Board and Melbourne Water provided funding for my trip to France in 1992. Lynda Entwisle assisted with French translations, including the abstract.

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